Sex in the Conjugatae and the relative frequency of the different types of conjugation

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It has been much disputed in the past whether there is a true sexual differentiation between the cells that fuse in the process of zygospore formation as found in the filamentous Conjugatae. Bessey (2) and others have argued that the process probably is sexual in cases of scalariform conjugation at least. Bennett (1) says: "I do not myself entertain any doubt that even in lateral conjugation there is an incipient differentiation of sex, although this differentiation extends only as far as the individual cells." The Wests (6) have gone even farther, and say, "against the sexuality of the Zygnemeae only two plausible objections can be raised; these are the phenomena of *lateral* and *cross-conjugation*," but they conclude that there is no reason even on these grounds to regard the Zygnemeae as other than sexual. Regarding the Mesocarpeae however, they say further that "indications of sexuality . . . are much less marked than in the Zygnemeae," and, "as these scarcely appreciable indications of sexuality are often absent, we may regard the Mesocarpeae as having lost almost all traces of differentiation into male and female gametes." Still later, G. S. West (7, p. 135) discusses the question as follows: "The term 'sexual' is often used to embrace all forms of gamogenesis, and is in this sense firmly established in botanical literature. It would, however, be more scientifically accurate to distinguish between gamogenesis (or the mere fusion of gametes) and sexual reproduction in the narrower sense (which should be restricted to those cases where there is a fusion of clearly differentiated ♂ and ♀ gametes). From this point of view, therefore, gamogenesis although including sexual reproduction is not identical with it. It must be remarked, however, that the gradation is so fine, especially in the Chlorophyceae, that the distinction is scarcely worth making. Sometimes, as in many of the Zygnemaceae, the gametes are morphologically indistinguishable but physiologically differentiated,

and in these cases there is often a morphological differentiation of the gametangia." The question certainly arises whether we ever find cases of reproduction by cell fusion as contrasted with reproduction by cell division in which the process is not to be considered as involving the essential features at least of sexual reproduction. We have obviously come to think of sexuality as involving some fundamental difference between the cells that fuse or conjugate, and consequently when we can find no visible difference between the gametes and can not in any way tell the male from the female, we find ourselves inclined to doubt the so-called sexual nature of such a conjugation. This is the case for all species of filamentous Conjugatae that form their spores midway between the two conjugating cells (TABLES II and IV) and the common doubt as to the sexual nature of this conjugation is expressed by the above quotation from West. Naturally among low plant forms of this kind we should expect to find the most primitive kind of sexuality in its most fundamental expression. Many of our fundamental ideas regarding the nature of sex processes we owe to the study of these very algal forms. Schmitz in 1879 saw two nuclei in a zygospore of *Spirogyra* "approach each other and fuse to a single nucleus." This was the first description of the nuclear behavior in the sexual process in the plant kingdom and was made before any such process was known to occur in any of the higher plants. It is certainly possible that by the intensive study of these primitive forms we may further clarify our ideas as to the nature and origin of sex.

Wittrock (8) has defined a zygospore as "a spore formed by an act of fecundation in which two or more cells of the same kind, not sexually different, have participated." Can we accept such a definition, and at the same time accept conjugation in these forms as being essentially a fecundating reproduction? If we can, the formation of gametes can involve only the difference between somatic cells as such and gametes, as such, rather than any essential difference between the two gametes themselves. Perhaps, after all, cells fuse rather because they are alike than because of an inherent difference between them. Certainly both of a pair of fusing cells in *Spirogyra* differ in some way from the somatic cells from which they arose. Such differences between

gametes as those of size and motility are perhaps to be considered as mere adaptations introduced in evolution to facilitate the bringing together of the two elements. Tröndle (5), for example, claims to have proved that the vegetative cells of the *Spirogyra* filament are haploid; then the difference, in the case of *Spirogyra* at least, between somatic cells and gametes can not be one of chromosome number, but some difference there must be to inhibit further vegetative division in any given cell of a filament and cause instead a union of that cell with another which has undergone a similar change. The gametic nature of any cell in a filament would then be fixed when it ceases to have the power to divide but instead has a new found power to unite with some one of its fellows. At that moment the cell ceases to be a somatic cell and becomes a gamete.

Cunningham (3) has reviewed the literature of the sexuality of *Spirogyra* rather thoroughly, but he throws out the cytological evidence of Tröndle when he compares the filament of *Spirogyra* with the sporophyte of higher plants. He concludes that "reduction may occur in the zygote, in which case a filament wholly of one sex arises, or reduction may occur just previous to reproduction, in which case . . . . . filaments of a bisexual nature are produced, which would conjugate either laterally or by cross-conjugation." Two of the species described by Tröndle as having the reduction take place in the zygote, would therefore according to Cunningham produce filaments "wholly of one sex," which however are known to conjugate in both the lateral and scalariform manners (see TABLES I and III). These are *S. longata* and *S. neglecta*. The real evidence of fecundation in these forms is not to be found in a visible or measurable difference between the filaments or even between the cells that fuse, nor is it to be found in the method of conjugation, whether lateral, scalariform, or cross conjugation, but it lies in the newly achieved possibility of fusion itself with resultant doubling of the nuclear material and the subsequent reduction division, which as far as the evidence extends at present takes place on the germination of the zygospore. If we believe that similarity between gametes favors rather than hinders fusion, then there is nothing at all startling in considering lateral conjugation as a fertilization even if the cells taking part are sister

cells, and nothing startling in considering the conjugation in all the species of the Mesocarpeae as fecundation. Even a case such as that described by Petit (4) for *S. mirabilis*, where he says that the contents of a single cell separate into two parts which reunite forming a spore, might be considered as a fertilization. There may also be an explanation here for many of the so-called aplanospores and parthenospores, which when the facts are fully known may be found to go through some process similar to that described by Petit for *Spirogyra* or by Woodruff for *Paramoecium*.

My purpose in gathering together the subtended tables has been to show the relative frequency of the different types of conjugation as shown in the literature. It is obvious that lateral conjugation is very common. This fact, together with occasional observations of cross conjugation, and the fact that both lateral and scalariform conjugation are often found not only in the same species, but in one and the same filament, go to prove that the individual cell rather than the filament should be regarded as the unit when the fusions in these forms are being considered. It is of course quite impossible in the present state of our knowledge to estimate finally the validity of many of these species. No claim is made for the completeness of the tables nor that all synonyms have been eliminated. In my opinion, however, they show approximately the proportions in which the different types of conjugation have so far been described in the literature and may be useful to students of the general problems of sex.

The principal sources of the tables are such standard works as Wolle, Hassall, Cooke, Petit, De Toni, West and Collins (as indicated in parentheses), although numerous shorter papers have also been consulted. Acknowledgment is due Dr. R. A. Harper for suggestions leading to the compilation of the tables. Species which do not appear are omitted because no drawing or definite statement as to the method of conjugation could be found in the literature.

TABLE I

CONJUGATION SCALARIFORM, SPORE IN ONE OF THE CELLS

Zygnema affine (Hassall)	*Zygnema cylindricum* (Transeau)
" *anomalum* (Wolle)	" *cruciatum* (Wolle)
" *chalybeospermum* (West)	" *cyanospermum* (Cleve)
" *Collinsianum* (Transeau)	" *ericetorum* (West)

Zygnema insigne (Wolle)
" *leiospermum* (Cooke)
" *peliosporum* (Wittrock)
" *purpureum* (Wolle)
" *rhynchonema* (West)
" *spontaneum* (West)
" *stellinum* (Wolle)
" *Vaucherii* (Cooke)
Spirogyra adnata (Wolle)
" *affinis* (Fritsch)
" *angolensis* (West)
" *arcta* (West)
" *bellis* (Petit)
" *Borgeana* (Transeau)
" *calospora* (Wolle)
" *catenaeformis* (Petit)
" *circumlineata* (Transeau)
" *communis* (Wolle)
" *condensata* (Wolle)
" *crassa* (Wolle)
" *cylindrospora*
" *daedalea* (Transeau)
" *decimina* (Petit)
" *diluta* (Wood)
" *dubia* (Wolle)
" *ellipsospora* (Transeau)
" *Farlowii* (Transeau)
" *flavescens* (Wolle)
" *fluviatilis* (Wolle)
" *fuscoatra* (Wolle)
" *gallica* (Petit)
" *gracilis* (Wolle)
" *Grevilleana* (Petit)
" *Hantzschii* (Wolle)
" *Hassallii* (West)
" *hydrodictya* (Transeau)
" *illinoiensis* (Transeau)
" *inflata* (Cunningham)
Spirogyra insignis (Petit)
" *Juergensii* (Wolle)
" *jugalis* (Cooke)
" *Lagerheimii* (Wittrock)
" *laxa* (Petit)
" *longata* (Fritsch)
" *lutetiana* (Wolle)
" *majuscula* (Wolle)
" *maxima* (West)
" *micropunctata* (Transeau)
" *neglecta* (Petit)
" *nitida* (Cooke)
" *orbicularis* (Cooke)
" *orthospira* (Wolle)
" *parvispora* (Wolle)
" *porticalis* (Cooke)
" *pratensis* (Transeau)
" *protecta* (Transeau)
" *punctata* (Wolle)
" *quadrata* (Petit)
" *quinina* (Cooke)
" *rectangularis* (Transeau)
" *reflexa* (Transeau)
" *rivularis* (Wolle)
" *setiformis* (Wolle)
" *serratum* (Hassall)
" *Spreeiana* (Petit)
" *subaequa* (Wolle)
" *subsalsa* (Wolle)
" *submaxima* (Transeau)
" *tenuissima* (Petit)
" *ternata* (Petit)
" *varians* (Wolle)
" *velata* (West)
" *Weberi* (Petit)
" *Welwitschii* (West)
Plagiospermum tenue (Wolle)
Sirogonium stricta (Wolle)

TABLE II

CONJUGATION SCALARIFORM, SPORE IN THE CONJUGATION TUBE

Zygnema Collinsianum (Transeau)
" *parvulum* (Wolle)
" *pectinatum* (Wolle)
" *Ralfsii* Wolle)
Zygogonium aequale (Wolle)
" *Agardhii* (Wolle)
" *decussatum* (Wolle)
" *ericetorum* (Cooke)
" *gracile* (Cooke)
" *rhynchonema* (West)
" *terrestre* (Wolle)
Mougeotia angolensis (West)
" *Boodlei* (West)
" *calcarea* (Wittrock)
" *capucina* (West)
" *delicatula* (Wolle)
" *divaricata* (Wolle)
" *genuflexa* (Collins)
Mougeotia glyptosperma (Wolle)
" *gracillima* (Wittrock)
" *irregularis* (West)
" *laetevirens* (West)
" *laevis* (Cooke)
" *minnesotensis* (Wolle)
" *numuloides* (Wolle)
" *parvula* (Wolle)
" *pulchella* (Wittrock)
" *quadrata* (West)
" *sphaerocarpa* (Wolle)
" *tenuis* (Wittrock)
" *tumidula* (Transeau)
" *uberosperma* (West)
" *verrucosa* (Wolle)
" *viridis* (Wittrock)
Mesocarpus crassus (Wolle)
" *depressus* (Cooke)

Mesocarpus macrosporus (Wolle)
" *radicans* (Wolle)
" *recurvus* (Wolle)
" *robustus* (Wolle)
" *scalaris* (Wolle)
Debarya africana (West)
" *americana* (Transeau)
" *calospora* (West)
" *decussata* (Transeau)
Debarya desmidioides (West)
" *glyptosperma* (Wittrock)
" *Hardyi* (West)
" *laevis* (West)
" *immersa* (West)
" *reticulata* (West)
Pyxispora mirabilis (West)
Temnogametum heterosporum (West)

TABLE III

CONJUGATION LATERAL, SPORE IN ONE OF THE CELLS

Zygnema insigne (Hassall)
" *leiospermum* (Cooke)
" *stellinum* (Wolle)
Mougeotia nummuloides (West)
" *parvula* (West)
Spirogyra affinis (Fritsch)
" *angulare* (Hassall)
" *bellis* (Cooke)
" *catanaeformis* (Petit)
" *communis* (Petit)
" *condensata* (Cooke)
" *crassa* (Cooke)
" *decimina* (West)
" *dubia* (West)
" *flavescens* (Cooke)
" *gracilis* (West)
" *groenlandica* (West)
Spirogyra Grevilleana (Petit)
" *Hassallii* (Wolle)
" *hydrodictya* (Transeau)
" *inflata* (Cunningham)
" *intermedia* (Hassall)
" *insignis* (Cooke)
" *Juergensii* (West)
" *longata* (Tröndle)
" *mirabilis* (Wolle)
" *neglecta* (Tröndle)
" *pratensis* (Transeau)
" *quadrata* (Cooke)
" *rectangularis* (Transeau)
" *Spreeiana* (Petit)
" *tenuissima* (Petit)
" *varians* (Petit)
" *Weberi* (Cooke)

TABLE IV

CONJUGATION LATERAL, SPORE IN THE CONJUGATION TUBE

Mesocarpus pleurocarpus (Cooke)
Mougeotia genuflexa (West)
Mougeotia mirabilis (Wolle)
Temnogametum heterosporum (West)

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